Using Movements and Habitat Utilization as a Functional Metric of Restoration for Estuarine Juvenile Fish Habitat

Authors: Freedman, Ryan M., Espasandin, Carrie, Holcombe, Erika F., Whitcraft, Christine R., and Allen, Bengt J.

Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 8(8) : 361-373

Published By: American Fisheries Society

URL: https://doi.org/10.1080/19425120.2016.1161681

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 8:361–373, 2016
Published with license by the American Fisheries Society
ISSN: 1942-5120 online
DOI: 10.1080/19425120.2016.1161681

ARTICLE

Using Movements and Habitat Utilization as a Functional Metric of Restoration for Estuarine Juvenile Fish Habitat

Ryan M. Freedman,*[1] Carrie Espasandin,[2] Erika F. Holcombe,
Christine R. Whitcraft, and Bengt J. Allen
Department of Biological Sciences, California State University–Long Beach, 1250 Bellflower Boulevard,
Long Beach, California 90840, USA

David Witting
National Oceanic and Atmospheric Administration, Southwest Regional Office,
501 West Ocean Boulevard, Long Beach, California 90802, USA

Christopher G. Lowe
Department of Biological Sciences, California State University–Long Beach, 1250 Bellflower Boulevard,
Long Beach, California 90840, USA

Abstract

Resource managers use habitat restoration to offset estuarine habitat loss; however, there is limited information about how functionally successful restorations have been, particularly with respect to their use by mobile marine predators. Restoration monitoring efforts typically use point-of-capture metrics to assess fish community recovery and habitat use, but this provides little insight into how fish habitat use changes through time. Using translocation experiments, we integrated the movements of California Halibut *Paralichthys californicus*, a conservation target species, into a point-of-capture monitoring program in a restored tidal creek estuary. Large halibut (>25 cm) were captured more frequently in the main stream channel, while small ones (<25 cm) were typically caught in the innermost marsh creeks. We actively tracked these fish (*n* = 20; size range = 26.6–60.5 cm TL) acoustically to identify their preferred habitats and challenged these habitat associations by means of translocations to a different habitats. Large fish tended to have small localized convex hull activity spaces, remaining in areas with high water flow and sandy substratum near eelgrass *Zostera marina* beds. Individuals that were translocated to marshes returned to the channel and exhibited movements over long distances from their initial locations to their last tracked positions; however, fish that were translocated from marshes to the channel remained in channel habitat and moved smaller distances between their first and last tracked points. Large halibut likely selected the channel because higher water flow would lead to higher concentrations of prey. Small halibut used marshes more frequently, likely because marshes have temperatures thought to maximize growth rates. Our study can serve as a proof of concept that linking point-of-capture and tracking data provides valuable information for habitat restoration, including the fact that California Halibut utilize estuaries in a

---

Subject editor: Kenneth Rose, Louisiana State University, Baton Rouge

*Corresponding author: ryanfreedman2@gmail.com
[1] Present address: Channel Islands National Marine Sanctuary, University of California–Santa Barbara, Ocean Science Education Building 514, MC 6155, Santa Barbara, California 93106-6155, USA.
[2] Present address: College of Southern Idaho, 315 Falls Avenue, Twin Falls, Idaho 83301, USA.

Received August 18, 2015; accepted March 1, 2016

size-segregated manner based on environmental conditions. This suggests that tidal creek estuaries with a variety of channel types and morphologies—like our study site—are well-suited to support this species.

Estuaries provide nursery habitats for many recreationally and commercially valuable fish species (Nobriga et al. 2005; Allen et al. 2006; Dahlgren et al. 2006), and in Southern California seasonally greater prey abundances and temperatures in estuaries are thought to promote faster growth rates of fish (Allen et al. 2006; Espinoza et al. 2011; Farrugia et al. 2011). Because microhabitat conditions (submerged aquatic vegetation, intertidal mudflats, and emergent vegetation) allow estuaries to host juvenile fish at higher densities and increase their feeding and growth potential per unit area, these habitats are better suited to support specific fishery stocks than are exposed coastlines (Irlandi and Crawford 1997; Allen et al. 2006; Fodrie and Mendoza 2006).

Despite the importance of estuaries as fish habitat, coastal development in California has contributed to a loss of approximately 90% of the state's estuarine and wetland habitats (Larson 2001). Fishery losses and associated changes in biodiversity along the coast of California, in conjunction with increased regulatory pressure to mitigate continued development, have resulted in increased support for estuarine wetland restoration over the last 20 years (Zedler 1996; Zedler et al. 2001). However, the long-term (>10-year) recovery rates of fish populations in restoration projects are still poorly understood (Zedler 1996). The limited availability of natural, unaltered estuaries to use as reference sites, along with habitat design differences between sites, make it difficult to quantify the postrestoration rates of ecological recovery (Zedler and Langis 1991; Zedler 1996; Nicolas et al. 2010a, 2010b).

Due to the variation among sites, the choice of evaluation metrics is crucial for effective comparisons among estuaries and for the adaptive management of fisheries. The recovery of estuarine fish communities is typically assessed by means of structural (in this case, instantaneous capture or point-of-capture) metrics such as species richness, diversity, and composition. However, these metrics fail to measure ecological functions (defined here as specific ecological processes) such as nutrient cycling, landscape connectivity, and secondary biomass production that are critical to supporting resilient and robust fishery stocks (Ambrose and Meffert 1999; West and Zedler 2000). Using structural metrics alone may limit the ability of resource managers to determine how fish respond to restored estuaries, as they reveal little about the length of time that or degree to which species use different estuarine habitats. These missing data are particularly challenging for assessing the recovery of fish communities, as species-specific habitat use patterns in estuaries may change over time (e.g., diurnally, tidally, seasonally, or ontogenetically) regardless of restoration succession state (Espinoza et al. 2011; Farrugia et al. 2011).

To complement structural metrics, functional metrics based on fish movement (e.g., residence time, rate of movement, tortuosity of a fish's movement, and area of use) or diet (e.g., stomach contents and stable isotopes) can be used to assess ecological processes relevant to target species and to infer the connectivity potential of different microhabitats. Although tracking animal movements is challenging, tracking data can provide high-quality, fine-scale information on how individuals use different habitats through time and their site fidelity in restored areas (Calabrese and Fagan 2004). For example, knowing fish's residence times and uses of space can help us to understand the environmental conditions that influence habitat selection and emigration so as to better assess whether restored habitats meet resource needs (Marsh et al. 2004; Espinoza et al. 2011; Farrugia et al. 2011).

The goal of this study was to provide a proof-of-concept example of how emigration, habitat selection, and space use data can be combined with traditional monitoring techniques to assess the relative abundance, size structure, habitat associations, and movements of juvenile and adult California Halibut *Paralichthys californicus*. California Halibut are a commercially and recreationally important ambush predator species in California (Love 2011). Temperature, depth, water flow, and salinity all influence their spatial distribution in estuaries (Madon 2002, 2008; Fodrie and Mendoza 2006); however, point-of-capture data provide little insight into how these factors affect their short- and long-term habitat use. Therefore, we set out to integrate a traditional monitoring plan using different point-of-capture techniques with a short series of active tracks to elucidate behaviors that might shape habitat selection and connectivity between microhabitats. We tested the habitat associations seen in the point-of-capture metrics through a small number of active tracks and translocation experiments. Estuarine restoration projects in Southern California often stipulate that increasing nursery habitat for California Halibut is a key objective (NOAA 2005); therefore, a clear understanding of how habitats are used by all halibut life stages is key to a successful restoration project.

STUDY AREA

The Huntington Beach Wetlands Complex (HBWC) is a 77-ha restored coastal salt marsh divided into three wetland sections (the Talbert, Brookhurst, and Magnolia marshes) that are connected to the ocean and each other by an armored flood control channel (Figure 1). The channel is the closest to the ocean inlet (the incoming water source) and is dominated by sand and shell hash substrata with a patchy mosaic of eelgrass *Zostera marina*. It is deepest near the inlet (>3 m) and progressively shallower (<1 m at its shallowest) with increasing distance into the estuary. The average width of the channel is 4.5 m off Talbert Marsh and 18 m off Brookhurst and Magnolia

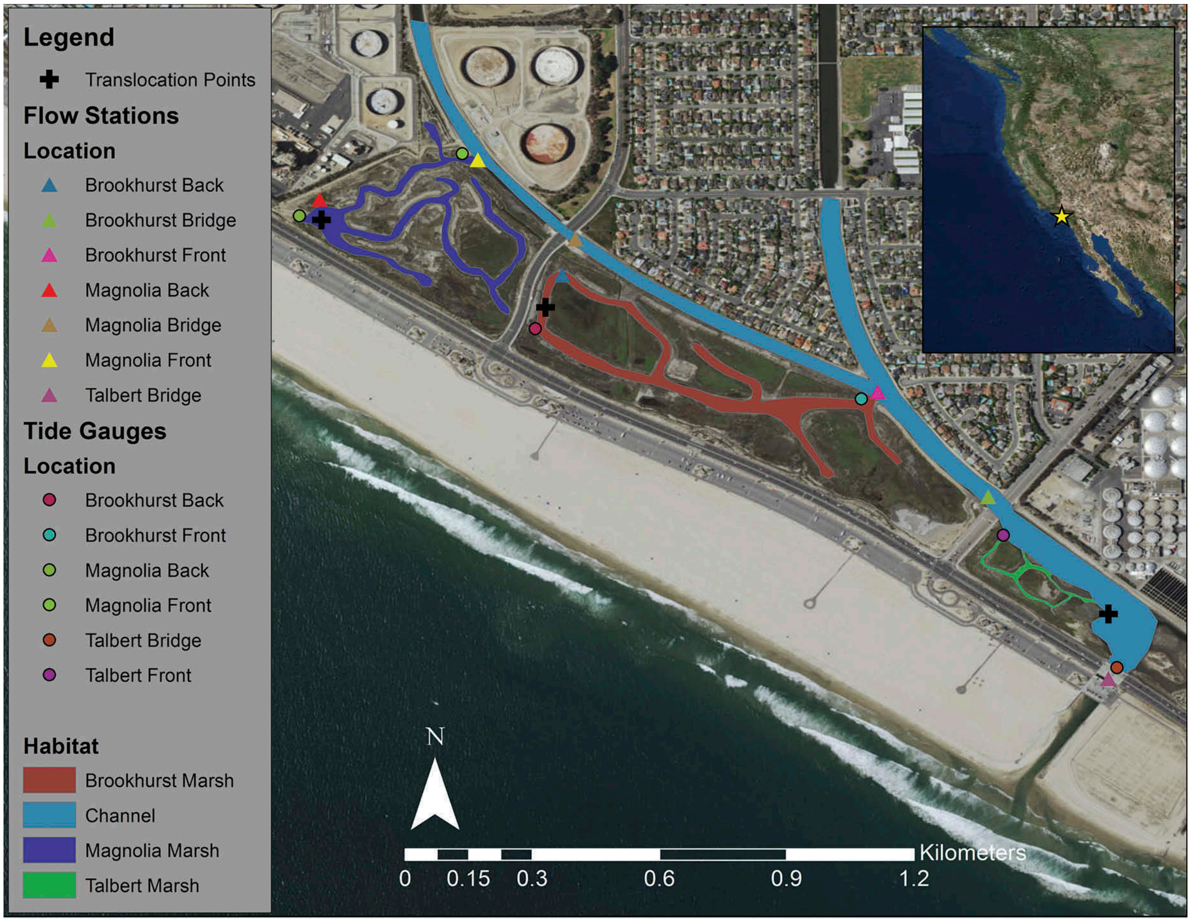

FIGURE 1. Image of the Huntington Beach Wetlands Complex (HBWC) showing the different marsh and channel habitats.

marshes (including the slope of the recontoured banks). Talbert Marsh (restored to full tidal flow in 1989) is dominated by shallow (0.25–1.5 m below mean low lower water height [MLLW]), narrow (<1.5-m) intertidal marsh creeks and mudflats that are totally exposed at low tide in all areas except those immediately adjacent to the channel. Brookhurst Marsh (restored to full tidal flow in 2009) combines intertidal mudflats with a marsh creek system comprised of subtidal channels approximately 3 m wide with a depth of 0.5–2.5 m below MLLW. Magnolia Marsh (restored to full tidal flow in 2011) includes a 0.39-ha subtidal basin and adjoining subtidal creeks (approximately 2 m wide and 0.5–2.5 m below MLLW) that remain inundated throughout the year.

METHODS

Table 1 provides an overview of when environmental monitoring and fish sampling were conducted.

Environmental monitoring.—Two Ruskin tide gauges (Model TGR-2050P, 0–10 m working depth; RBR, Ltd.) were deployed at 1-month intervals among six fixed locations in the HBWC (Figure 1) from 2009 to 2013 to record water level and temperature every 10 min. The tide gauges were rotated among the six stations, which meant that at any given time only two stations had a gauge while the other four had no instrumentation. The locations of the gauges were changed each month to one of the previously vacant locations. Loggers were placed within 10 cm of the bottom to make sure water temperatures were recorded where California Halibut were most likely to occur. "Front" stations were located at the interfaces between the marshes and the channel, while stations at the most distant points of the marshes were known as "back" stations. (Because Talbert Marsh fully drains at low tide, there was no Talbert back station.) Talbert Bridge station was placed under the Pacific Coast Highway bridge approximately 300 m inland of the ocean inlet. Since California Halibut typically use estuaries during the summer months (Haaker 1975; Madon 2002; Fodrie 2006), the daily mean temperature data through the summer (May to September) were averaged by day and compared among locations using general linear modelling (GLM) with the date as a random blocking factor. Tukey's post hoc comparisons

TABLE 1. Frequency of sampling throughout the HBWC (M = monthly, Q = quarterly). Six point-of-capture sampling events took place during each day of sampling in each habitat. The letter X denotes research related to all other data collection that occurred during that time.

Metric type	Metric	2009	2010	2011	2012	2013
Point of capture	Beach seine	M	M	Q	Q	
	Hook and line		M	Q		
	Trawl	M	M	Q	Q	
Movements	Control group		X	X		
	Channel to Brookhurst		X	X		
	Channel to Magnolia				X	
	Magnolia to channel				X	
Environmental parameters	Eelgrass		X	X	X	
	Temperature	X	X	X	X	
	Water flow					X
	Geological		X	X	X	

were used to identify which sites differed with respect to mean temperature. The number of days with a maximum temperature above 25°C (an important temperature threshold identified by Madon 2002) were compared among sites by means of a chi-square test.

The velocity of tidally driven water flow was measured by stationing Sontek S4 river surveyors at seven different locations throughout the HBWC (Figure 1). Deployments lasted for at least 5 h at the same period in the tidal cycle within a time frame of 8 d in 2013. Measurements of water velocity were taken at the back of Brookhurst Marsh, the tidal basin of Magnolia Marsh, the entrances to Brookhurst and Magnolia marshes, and along three points in the channel at varying distances from the ocean inlet (one at Magnolia Bridge, one at Brookhurst Bridge, and one near the Pacific Coast Highway Bridge). Hourly means of water velocity measurements were compared between marsh and channel habitats by means of a Wilcoxon rank-sum test with continuity correction. Salinity was not included in the analysis, as Southern California estuaries are typically fully marine (HBWC ranges from 26‰ to 33‰) and have little freshwater input.

Eelgrass mapping.—In 2010, eelgrass beds were mapped by walking around the bed edges with a GPS handheld device. As this was not possible due to depth in 2010, an aerial Google Earth image was used to trace the outlines of eelgrass patches and cross-referenced with aerial photos taken at 1540 hours on October 9. Brookhurst Marsh was assumed to be devoid of eelgrass in 2010 because it was newly opened in 2009, an assumption that was verified through opportunistic checking. In 2011–2012, teams of four to five observers walked transects along submerged creek channels, took GPS points every 3 m, and recorded the presence or absence of eelgrass. In 2011 only Brookhurst Marsh was mapped, while in 2012 the entire HBWC complex was mapped excluding Talbert Marsh and the channel south of Brookhurst Street. Geological substrata (e.g., mud, sand, and shell hash) data were qualitatively recorded in 2011 alongside eelgrass mapping by means of core samples and visual observation.

California Halibut population survey methods.—Our study was not designed to determine the size of the California Halibut population found within the HBWC. The mix of gear types that we used was selected to efficiently sample all of the HBWC with its differing habitat complexity, and therefore the data are not comparable and cannot be combined to obtain a strong, local population estimate. Instead, relative abundance estimates (counts of individuals) are presented to aid in the interpretation of the movement data and in the qualitative inference of habitat preferences. Relative halibut abundance, distribution, and size structure are based on three sampling techniques: hook-and-line, beach seine, and beam trawl surveys. For the hook-and-line surveys, two teams of two fishers haphazardly selected locations on the water's edge during a >1.21-m tide height in all four of the HBWC habitats from 2009 to 2010 (see Table 2). Sampling locations were spread evenly across habitats, with six stations being selected in the marshes and six in the channel every day. In each location, fishers were stationed approximately 10 m from each other and casted consistently for 20 min at approximately two casts/min using artificial lures (pink plastic grubtails with a 1-0 lead head hook size).

TABLE 2. Dates and total effort (min) for hook-and-line fishing for point-of-capture metrics, by location in the HBWC, 2010.

Date	Brookhurst Marsh	Channel	Talbert Marsh	Total
Jan 7	320	0	0	320
Feb 16	120	120	120	360
Feb 28				
Mar 15	240	240	240	720
Apr 7	280	240	240	760
May 30	120	120	120	360
Jun 25	240	240	240	720

Beach seines (33.5 m long × 2 m deep with 0.65-cm mesh) were deployed in a semicircular fashion by two people and drawn ashore at six selected locations that were spaced to ensure thorough coverage throughout each marsh. Sampling occurred at tidal heights above 0.61 m so that the seine could be deployed completely. Depth and current flow in the channel made the beach seining ineffective, so we discontinued such sampling in the channel after 24 deployments. Six beach seine deployments were made in each habitat on each sampling date, with locations being chosen haphazardly to spread the effort out across the entire subtidal habitat in each marsh. Beach seining was done monthly in each marsh from 2009 to 2010 and quarterly from 2010 to 2013. One hundred and thirty-eight seinings were done in Brookhurst Marsh, 132 in Talbert Marsh, and 48 in Magnolia Marsh.

A 1-m beam trawl (0.5-cm delta netting, 0.1-cm heavy delta chafing netting on the cod end) was towed for approximately 100 m at 1.02–1.54 m/s (2–3 knots) from a skiff within the channel for an estimated coverage of 100 m^2 per tow. Three samples were taken monthly in two areas from 2009 to 2010, i.e., south and north of the Brookhurst Bridge. Marsh creeks could not be sampled using the beam trawl due to their shallow depth and tortuosity. After 2009, beam trawl sampling continued on a quarterly basis.

All California Halibut caught during our surveys were measured for total length. Individuals more than 18 cm long were tagged with small T-bar anchor tags in the postcranial muscle tissue (FLOY Tag, Seattle) for identification upon recapture. The size frequency distributions of the fish caught were descriptively compared among gear types. Relative abundances estimated as counts from beach seine sampling were compared among years, marshes, and seasons by means of chi-square tests.

Tagging and capture procedure.—For active tracking studies, California Halibut were captured using hook and line or by beach seining independently of the population surveys (n = 20, size range = 26.6–60.5 cm). We only tagged fish >25 cm and externally fitted them with acoustic transmitters (VEMCO, V9-1L, 29 mm long, power output = 145–151 dB, battery life = 14 d, pulse interval = 2 s, frequency range = 63–84 kHz) by attaching tags to the postcranial musculature with sutures made out of chromic gut (similar to the tagging method in DeCelles and Cadrin 2010) or surgically implanting them into the body cavity. We assumed that fish of this size would be able to handle the tag burden, as researchers in other studies have tagged Winter Flounder *Pseudopleuronectes americanus* smaller than 19 cm (Fairchild et al. 2009) and other *Paralichthys* spp. at similar sizes compared to the halibut in our study (Furey et al. 2013). Surgical implantation of tags in other species of flatfish appears to have had no effects on feeding and activity behavior (Moser et al. 2005). Incisions from surgical implantations were closed with two interrupted chromic gut sutures (7-0, 6.5-mm needle; Ethicon, Inc.), and fish were allowed to recover in a cooler of fresh seawater prior to release (California State University–Long Beach, Institutional Animal Care and Use Committee protocol 290). Acoustic tags were deployed at different frequencies (63, 66, 75, 78, 81, and 84 kHz) so that there would be no sound collusions between tags, and tags with the same frequency were only deployed after the previous tag's battery had died to be certain which fish was being tracked at any given time. After release, individuals were tracked from either a skiff or a kayak using a directional hydrophone (VEMCO Model VH165) and acoustic receiver (VEMCO Model VR100). Fish's GPS positions were recorded every 10 to 15 min. Positions were typically taken within 2 m, since high signal strength could be verified with visual observation of the fish in most locations.

Tracking procedure.—We actively tracked individuals for 24-h periods to see whether the California Halibut exhibited a daily movement pattern that could inform the results of point-of-capture metrics, and we conducted a translocation experiment to compare individuals' habitat preferences with those seen in the point-of-capture data. We used an active telemetry approach to get fine-scale data to compare preferences with microhabitat habitat availability, which was not possible using passive telemetry. After the fish were tagged and released, individuals were tracked from either a skiff or a kayak using a directional hydrophone and acoustic receiver as noted above. Fish's GPS positions were recorded as described in the previous paragraph.

Four distinct groups of fish were tracked based on the treatment to which they were subjected prior to tracking: a control group (n = 7; no translocation; tracking conducted in 2009–2010), a channel-to-Brookhurst-Marsh translocation group (n = 7; 2010–2011), a channel-to-Magnolia-Marsh translocation group (n = 4; 2012–2013), and a Magnolia-Marsh-to-channel translocation group (n = 2; 2012–2013). The control group (26.6–60.5 cm) were caught, tagged, and released at their site of capture in the channel to test what habitats these fish used naturally. After release, fish were immediately tracked for 24 h and typically at least once more within 2 weeks of the first tracking. One fish (fish no. 1) was caught near Talbert Marsh but released at the entrance of Brookhurst Marsh (a shorter distance from the site of capture compared with fish that experienced a full translocation) shortly after the restoration was completed. The first 24-h tracking period for fish no. 1 was not used in any comparisons, as the displacement was not to a designated translocation spot and the movement from the location of capture may have altered the fish's behavior so much that it could not be considered a control; however, all subsequent tracks of fish no. 1 were included.

The majority of large California Halibut were associated with channel microhabitats both in the point-of-capture and tracking data. We wanted to test this habitat selection by translocating a small number of fish from their capture locations in the channel into different marsh creek habitats. The

Brookhurst Marsh translocation group (31.0–45.5 cm TL) were caught in the channel and then translocated to the distal end of Brookhurst Marsh (~1 km from their location of capture). The first few fish (*n* = 3) from the Brookhurst Marsh group were tracked for approximately 24 h. After exiting the marsh, all of these fish returned to the channel and remained in the same location for the remainder of the tracking period. Based on the behavior of these individuals, the remaining fish (*n* = 4) translocated to the distal end of Brookhurst Marsh were tracked only until they reached the channel; tracking efforts then ceased, as these individuals were assumed to remain in the same location. Tracking periods therefore ranged from approximately 9 to 16 h for the four more briefly tracked fish that returned to the channel less than 24 h after translocation. In 2012, we tracked the Magnolia Marsh translocation group (37.8–42.0 cm). These fish were caught in the channel, translocated to the Magnolia Marsh tidal basin (~1.8 km from the location of capture) and tracked for 24 h after release. Additionally, two fish in the channel translocation group were captured in Magnolia Marsh (41.0 and 46.3 cm), translocated to the channel habitat adjacent to the ocean inlet, and tracked for 24 h after release to test whether individuals were selecting specific habitats or just homing back to their locations of capture. Because California Halibut were rarely captured in marshes despite large amounts of effort, the size of the marsh-to-channel translocation group is small. A breakdown of tracking effort is given in Table 3.

Movement analysis.—Tracking data were filtered to eliminate GPS locations that plotted outside of possible aquatic habitat. To quantify potential habitat selection, the proportion of individuals that left their translocation site was compared with a 50% null distribution by means of a chi-square test. Euclidean distance analysis (EDA; Conner and Plowman 2001) was used to calculate the distances between habitat types (geological substrata and eelgrass edges) and (1) the locations of control groups and (2) randomly generated points. Ratios were calculated for each habitat type by dividing the mean distance from the observed locations to each habitat type by the mean distance from a randomly generated set of points to each habitat type. A multivariate analysis of variance (MANOVA; SAS 9.1.3, SAS Institute, Inc.) was used to test for random habitat use by the California Halibut by determining whether the EDA ratios were significantly different from 1 (which indicates that habitat use is proportional to its availability). Fixed-point localized convex hull (LoCoH) activity spaces were created in the ADEhabitat package in R (R Core Team 2013; Calenge 2015) for tracks of at least 24 h. Two LoCoHs were created for each track: a 95% LoCoH (which is considered a measure of the overall daily activity space of an animal) and a 50% LoCoH (which is more representative of the area of core use). The LoCoH activity spaces were compared between control, marsh translocation, and channel translocation groups using a Kruskal–Wallis test with

TABLE 3. Treatment group, length, number of tracks, and total track time for each California Halibut tracked; LoCoH = localized convex hull. Please note the differences in the number of samples and the years of sampling in Table 1.

Fish	TL (cm)	No. of tracks	Hours tracked	Dates tracked	Group	LoCoH activity space created?
1	37.1	3	60	Aug 4–14, 2009	Control	Yes
2	28.7	3	60	Aug 13–21, 2009	Control	Yes
3	45.8	3	60	Sep 28–Oct 4, 2009	Control	Yes
4	52.2	2	48	Oct 23–28, 2009	Control	Yes
5	60.5	2	48	Dec 16–19, 2009	Control	Yes
6	29.9	1	34	Jan 10–11, 2010	Channel to Brookhurst	Yes
7	26.6	3	60	Mar 5–13, 2010	Control	Yes
8	44.5	2	33.5	Apr 8–18, 2010	Control	Yes
9	31.0	3	60	May 12–20, 2010	Channel to Brookhurst	Yes
10	45.5	3	60	Jun 14–23, 2010	Channel to Brookhurst	Yes
11	41.2	1	8.75	May 25, 2010	Channel to Brookhurst	No
12	38.8	1	11.25	May 26, 2010	Channel to Brookhurst	No
13	46.4	1	15.75	Jun 14, 2010	Channel to Brookhusrt	No
14	49.6	1	11	Jun 15, 2010	Channel to Brookhurst	No
15	37.8	2	48	May 27–Jun 3, 2012	Channel to Magnolia	Yes
16	43.0	2	48	Jun 4–7, 2012	Channel to Magnolia	Yes
17	46.3	2	48	Jun 14–19, 2012	Channel to Magnolia	Yes
18	40.5	2	48	Jun 22–29, 2012	Channel to Magnolia	Yes
19	41.0	2	48	Jul 2–7, 2012	Magnolia to channel	Yes
20	44.9	2	48	Jul 10–15, 2012	Magnolia to channel	Yes

Siegel and Castellan's post hoc multiple comparisons. A net track distance metric (NTD) was also calculated for 24-h tracks by taking the Euclidean distance between the beginning and ending points of the track. The NTDs were compared among the same control, marsh translocation, and channel translocation groups using a Kruskal–Wallis test and Siegel and Castellan's post hoc multiple comparisons.

RESULTS

Environmental Monitoring

Average daily water temperatures from May to September were significantly different among sites (Figure 2; GLM: $F_{5,\ 622} = 259.5$, $P < 0.001$). Waters were generally warmer farther from the ocean inlet. Talbert Bridge had the coolest water measured (mean = 19.78°C, range = 16.8–23.83°C), likely due to its proximity to incoming ocean water, while all other sites had means around 21°C (range = 21.0–21.6°C). The maximum temperatures at Magnolia back, Brookhurst back, and Magnolia front were all approximately 2°C warmer than the maximum water temperature at the Talbert Bridge station. The number of days with water temperatures >25°C were significantly different by site ($\chi^2 = 24.31$, df = 5, $P < 0.001$); sites farther from the ocean inlet tended to have more days above this threshold. Magnolia back ($n = 28$ d) had more than twice as many days with temperatures >25°C than any other site. Water velocity (tidal flow) was significantly higher in the channel (median = 0.08 m/s, range = 0.04–0.50 m/s) than in marsh habitat (median = 0.03 m/s, range = 0.01–0.06 m/s) (Figure 3; Wilcoxon test: $W = 490$, $P < 0.001$).

Eelgrass Distributions

Immediately following the restoration of tidal flow in 2009, eelgrass coverage in Brookhurst Marsh was 0%. In June 2010, the subtidal habitats available in the HBWC were categorized into three geological substratum classifications: mud (53%), sand (46%), and shell hash (1%). The channel was dominated by sand and shell hash (~95%), whereas the marsh subtidal areas were comprised of sand (~35%) and mud (~65%). In 2010, the eelgrass in Brookhurst Marsh covered approximately 16% of the subtidal, area increasing to 45% by 2012 (Figure 4). Similar expansion was observed in Magnolia Marsh, where eelgrass coverage was negligible in 2011 (the year it was first opened to tidal flow) but expanded to 12% by 2012.

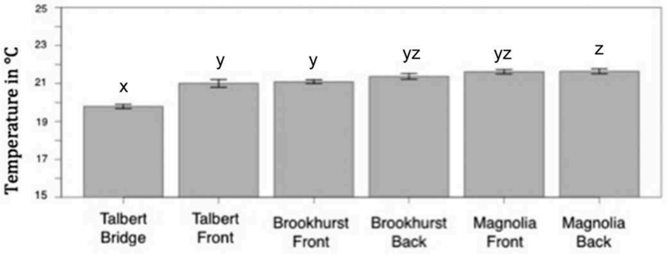

FIGURE 2. Mean summer temperatures by site in order of their distance from the ocean inlet (GLM; $F_{6,\ 622} = 259.50$, $P < 0.001$); error bars = SDs. Different letters indicate statistically significant differences among treatments at the 0.05 level as determined by Tukey's honestly significant difference test.

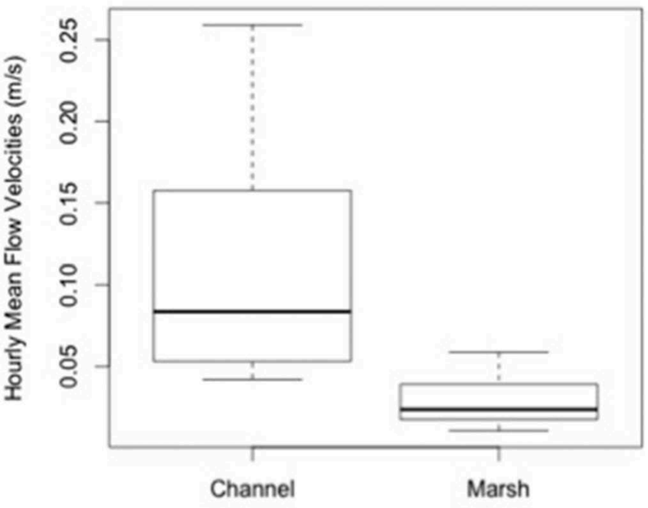

FIGURE 3. Hourly mean flow velocity measurements in the channel and in Brookhurst and Magnolia marshes (combined). The black lines within the boxes represent the medians, the box dimensions the second and third quartiles, and the whiskers the first and fourth quartiles.

Halibut Population Distribution

Across all methods, large California Halibut were not typically captured in the marshes but were captured in the channel (Table 4; Figure 5). Relative to the other methods, hook-and-line fishing was biased toward larger sizes of fish (Figure 6), and no large individuals were ever captured by this method in marsh habitat. By contrast, small halibut were consistently captured in marsh habitat, with the majority of these being captured with beach seines (Table 4; Figure 6). This trend held across years for both large and small halibut (Table 3; Figure 5). When the data were pooled across seasons, most of the fish caught in the marshes were under 25 cm and these such individuals were rarely captured in the channel. This apparent ontogenetic shift remained consistent among years as well.

The relative abundances of California Halibut in beach seines differed among years, with the number in 2011 (5) being much lower than those in 2009 (27), 2012 (42), and 2010 (56) ($\chi^2 = 43.97$, df = 3, $P < 0.001$). However, sampling effort dropped from monthly sampling in 2009 to quarterly sampling in subsequent years, which would inflate the relative abundance in 2009. We only used beach seine data for the comparison among years because of the relatively small numbers of halibut caught using other methodologies and the limited spatiotemporal range of the other point-of-capture data sets. The relative abundance of halibut in beach seines was over five times as great during the summer season

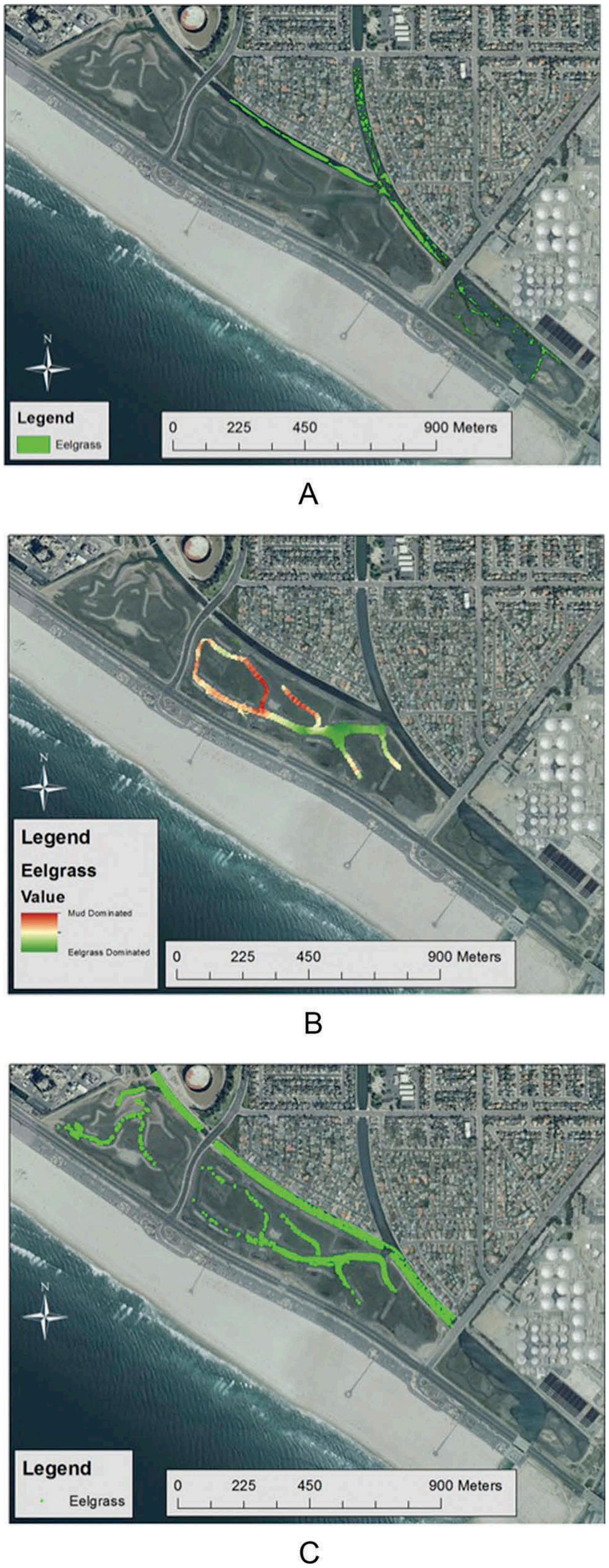

FIGURE 4. Images showing the eelgrass coverage in the HBWC in **(A)** 2010, **(B)** 2011, and **(C)** 2012. Different metrics are used due to differences in the sampling protocols among years.

(89 individuals) as in the next highest season (the spring season, in which 16 individuals were captured).

Fish Movements

All of the fish caught in channel habitat and translocated to either Brookhurst or Magnolia Marsh returned to the channel, and all but one fish (fish 15) displayed this behavior within the first 24 h. Fish 15 was detected 2 d later in channel habitat and remained in the channel for the duration of a subsequent 24-h track. In contrast, both of the fish that were caught in Magnolia Marsh and translocated to the channel habitat remained in the channel for at least 24 h.

The larger California Halibut in the control group occupied shell hash, eelgrass ecotone (i.e., areas within 2 m of a different habitat type), and sandy substrata disproportionately to their availability (Table 5; MANOVA: Wilk's $\lambda = 0.005$, $F_{4,\ 6} = 327.31$, $P < 0.001$). Over half (54%) of all control group halibut positions were detected in the area that we considered eelgrass ecotone, even though eelgrass beds comprised only 16% of the total available benthic habitat at the time.

Fish translocated to channel habitat trended to have the smallest core areas (50% LoCoHs; median = 2.7 m^2, range = 2.7–3.9 m^2), while individuals translocated to marsh habitats had the largest ones (median = 23.8 m^2, range = 7.5–685.3 m^2) (see the Supplement available separately online). The difference among groups was nearly significant (Figure 7A; Kruskal–Wallis test: $\chi^2 = 5.86$, df = 2, $P = 0.053$). However, there was no difference in the size of daily activity space (95% LoCoHs) among individuals from the marsh, channel, and control groups (Figure 7B; $\chi^2 = 2.85$, df = 2, $P = 0.233$).

We found significance differences in NTDs among groups (Figure 8; Kruskal–Wallis test: $\chi^2 = 11.27$, df = 2, $P < 0.003$). Pairwise comparisons revealed that marsh-translocated fish had significantly larger NTDs (median = 502 m, range = 56–758 m) than both channel-translocated fish (median = 11 m, range = 11–21 m; observed difference = 12.28 m, critical difference 0.05 [i.e., the value observed values need to exceed in order to be statistically significant]). Marsh-translocated California Halibut typically moved from their translocation spot until they reached the channel, at which point they remained in approximately the same location for the remainder of the track.

DISCUSSION

Juvenile California Halibut are thought to use seasonally warm, prey-abundant estuaries to maximize their growth and survival before recruiting to adult stocks (Allen et al. 2006; Fodrie and Mendoza 2006; Fodrie and Levin 2008). Halibut typically reach reproductive maturity at 59 cm for females and 32 cm for males, which means that the majority of the fish in our study were likely juveniles (Love and Brooks 1990). Prior studies found that some juvenile halibut that originally recruited to open coastal waters later moved into estuaries.

TABLE 4. Number (ranges in parentheses) of California Halibut captured, by location and gear type. Due to differences in sampling efficiency among the collection methods, the values cannot be standardized and compared quantitatively. The values do not include the halibut that were acoustically tagged, as those fish were captured during an independent, nonstandardized fishing effort.

Location	Gear type	No. of samples	Fish <25 cm	Fish >25 cm
Marshes	Hook and line	229	0	0
	Beach seine	360	125 (1.1–29.0)	7 (34.1–60.5)
	Trawl	130	16 (2.6–20.3)	0
Channel	Beach seine	24	2 (7–17.8)	0
	Hook and line	96	0 (27.4)	5 (32.0–51.3)

Juvenile halibut that did not migrate to estuaries had markedly lower survival rates than those that resided in estuaries (Kramer 1990). Our study supports the notion that estuaries are seasonal nurseries, as the number of halibut caught in the HBWC during summer months was over five times the number captured in other seasons. However, our telemetry and capture data support the notion that habitat use by halibut is size-segregated in terms of a number of habitat factors, which may have implications for designing restoration projects to better support halibut stocks.

Our data suggest that large California Halibut select channel habitat over marsh habitat. Large halibut were frequently caught on hook-and-line gear in the channel, whereas no large halibut were caught by that method in the marsh creeks, despite considerable effort. When we tested this habitat association by means of telemetry, no tracked fish made forays into

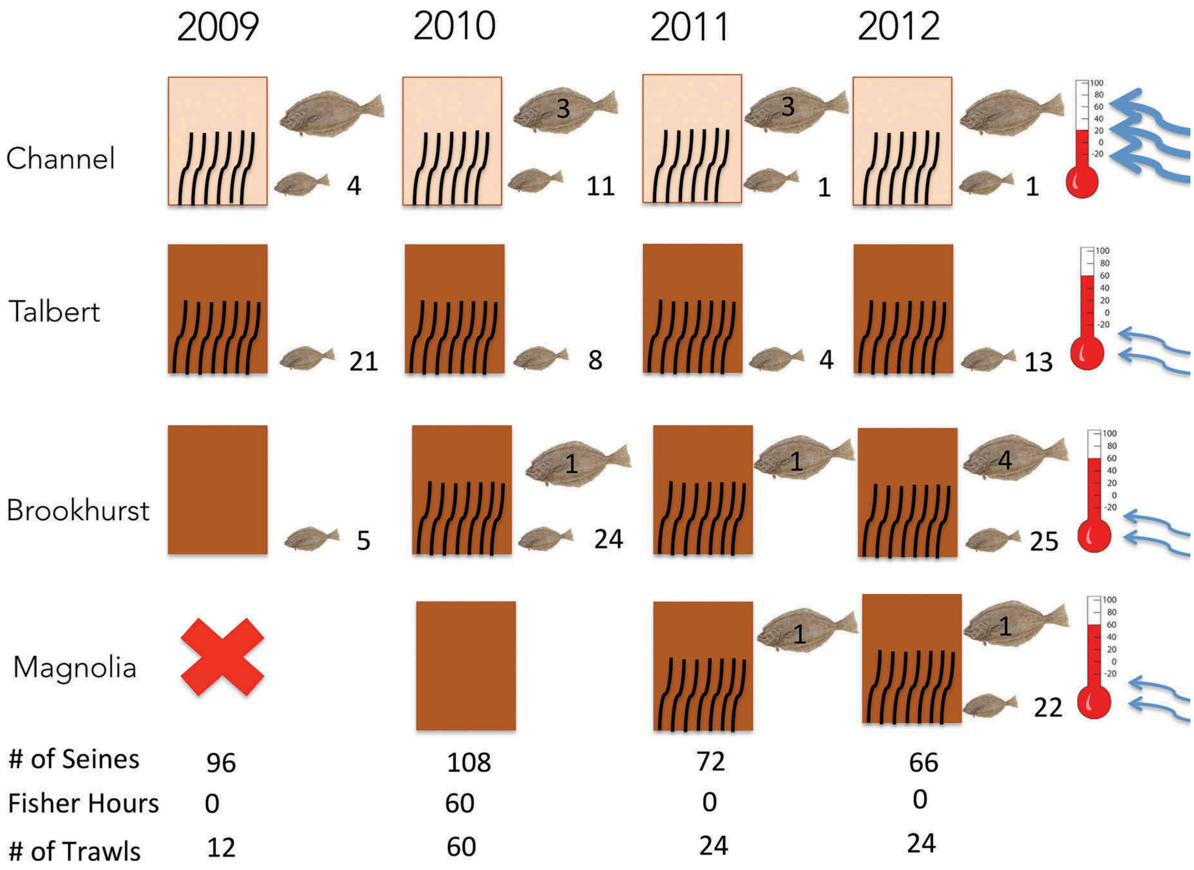

FIGURE 5. Schematic showing the presence or absence of California Halibut for all capture methodologies and habitat conditions in each microhabitat. Light tan squares indicate sand habitat, dark brown squares mud habitat. Squiggly lines within the squares indicate the presence of eelgrass that year. The thickness of the blue lines indicates the rate of water flow and the thermometer gauges the relative temperatures. The presence of large halibut is indicated by the large fish icons, and presence of small halibut by the small fish icons. The numbers over and next to the icons indicate how many individuals of that type were captured across all point-of-capture methodologies; icons without numbers represent fish captured for telemetry studies outside of the quantified fishing time. The total fishing effort for each year is given at the bottom of the figure.

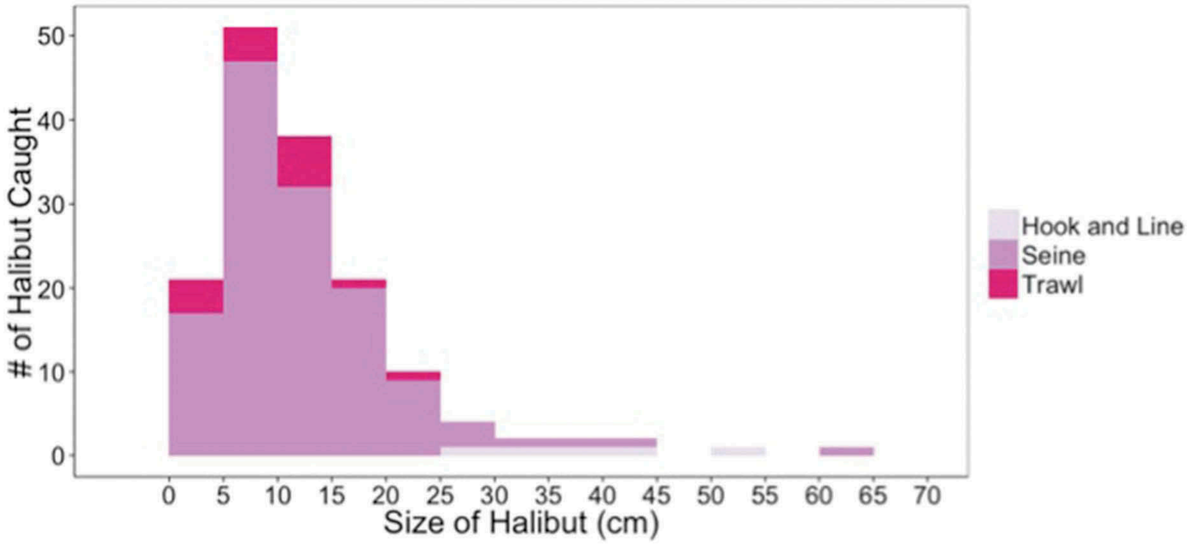

FIGURE 6. Stacked histogram of the total number of California Halibut captured in the HBWC, by size for each gear type.

marsh habitat. Although we had relatively low sample sizes, the lack of marsh habitat utilization was clear for both control and translocated large halibut. While in channel habitat, control halibut typically remained motionless and had smaller 50% LoCoH activity spaces and shorter NTDs in habitats that may lead to higher prey encounter rates (e.g., eelgrass ecotones and areas with high-velocity water flow) that were also dominated by sandy and shell hash substrata (Jordan et al. 1997; Kimmer et al. 1998; Leonard et al. 1998; Madsen et al. 2001; Hughes et al. 2002). The observed lack of movement and higher rates of capture of large halibut in the channel could be indicative of individuals' attempting to feed on prey carried into the estuary on incoming and outgoing tides (Haaker 1975; Love 2011). Since all of the water brought in from the ocean has to travel through the channel and the channel has the highest water flow rates in the HBWC, the halibut in the channel likely have higher encounter rates with prey than those at the back of marshes. Other studies have found a shift in diet for halibut at a similar size break, whereby larger individuals feed on more marine and fish prey (Fox 2013). This would further support the idea that larger halibut use the channel due to its higher prey encounter rates.

TABLE 5. Ratios of (1) the mean distances from observed California Halibut locations to each habitat type (eelgrass edge or sediment type) to (2) the mean distances from a randomly generated set of points to each habitat type.

Fish	Eelgrass	Shell hash	Sand	Mud
1	0.0739	0.0437	0.0113	1.5476
2	0.0501	0.0192	0.0139	2.1567
3	0.1952	0.9877	0.0025	0.8607
4	0.0925	0.0994	0.0059	1.6684
5	0.0332	0.0244	0.0152	2.0632
6	0.0356	0.0741	0.0059	1.6856
7	0.0456	1.2328	0.0088	1.4091
8	0.0962	0.0515	0.0112	1.5640
9	0.1690	0.6893	0.0015	1.1595
Mean	0.0879	0.3580	0.0085	1.5683

When we tested this habitat selection concept by means of a small set of translocation experiments, the fish immediately returned to the channel, leading to comparatively higher NTDs and core area sizes. These fish appeared to resume lie-and-wait feeding behavior when they reached the channel and exhibited limited movements after leaving the marshes. It is possible that the extremely small LoCoHs exhibited by the halibut translocated to the channel are indicative of a tagging or stress effect from translocation. However, this limited movement is not consistent across all tagged individuals and translocation groups and the California Halibut's ambush predator behavior could also lead to the limited movement that we observed.

Other flatfish, European Flounder *Platichthys flesus* and English Sole *Parophrys vetulus*, have been shown to exhibit site fidelity during summer months (Dando 2011; Moser et al. 2013). However, our translocated California Halibut did not return to their locations of capture but stopped once they had reached areas with environmental conditions similar to those where they had been captured. Because of this, we hypothesize that individuals select habitats based on a suite of environmental parameters instead of as a result of homing behavior.

The point-of-capture and movement metrics for California Halibut appear to be linked to environmental parameters such as

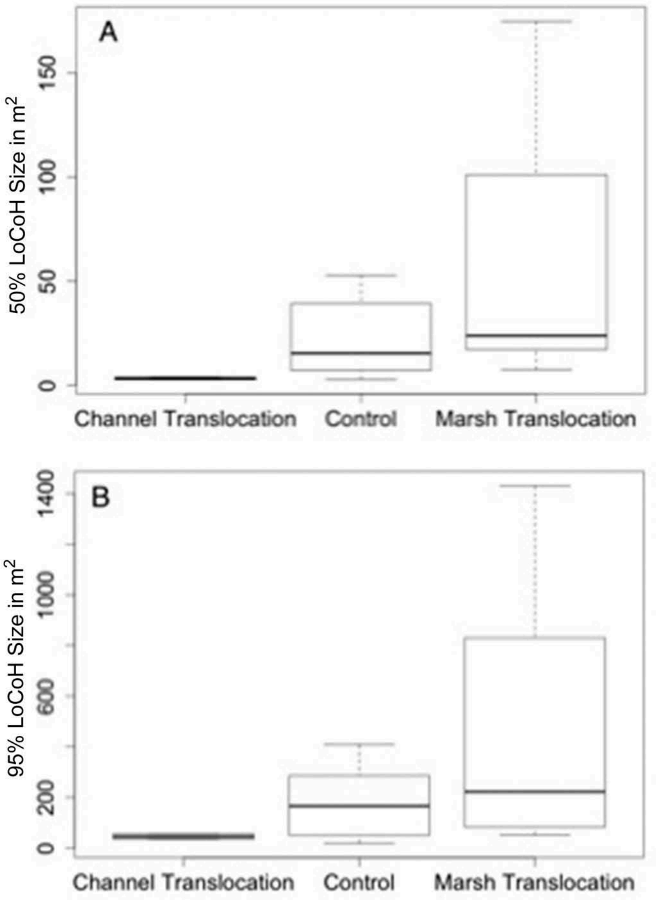

FIGURE 7. Box-and-whisker plots showing **(A)** the core area size and **(B)** the daily activity space among translocation groups.

water flow, the presence of an eelgrass ecotone, sediment characteristics, and water temperature. As mentioned before, the presence of eelgrass and increased water flow may drive large halibut to select the channel by increasing their prey encounter rates and feeding efficiency (Kimmer et al. 1998; Leonard et al. 1998; Merino et al. 2007). However, temperature may also be an important driver in the size-specific estuarine microhabitat selection that we see in our capture data. The median water temperature near Talbert Bridge (i.e., the location of translocation for fish translocated to the channel) was 19.6°C, which is close to the temperature that maximized growth and prey consumption among the large halibut (23.7–31.0 cm TL) observed by Madon (2002). The peak growth rate for halibut of this size-class is relatively restricted in terms of temperature (just a 5°C change leads to negative growth rates); thus, the small changes in water temperature from the channel to the backs of marsh creeks could be biologically relevant to halibut habitat selection.

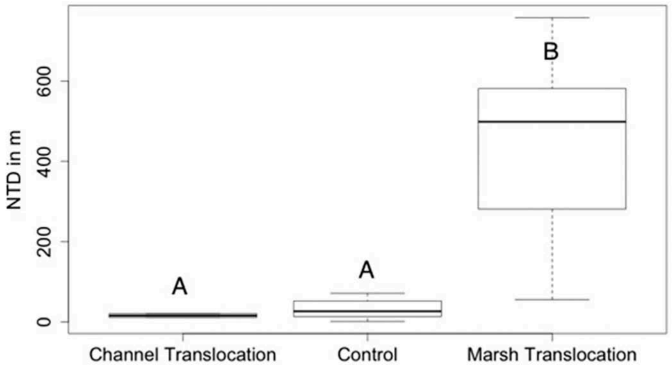

FIGURE 8. Box-and-whisker plots showing the net track distance (NTD) among translocation groups.

Conversely, a small California Halibut's (11.0–17.0 cm TL) metabolic, growth, and prey consumption rates are maximized at water temperatures similar to those found in marshes (Madon 2002). Our point-of-capture data show that halibut under 25 cm were more frequently found in the marsh habitat. This species' ontogenetic shift in temperature tolerance could be the major reason we see a split of size-classes within the HBWC. The diets of the small halibut caught in the channel were different from those of halibut caught in other habitats, which may reflect the habitat selection shift that we observed (Fox 2013). Optimal temperatures may contribute to the marshes' having higher numbers of small halibut despite the lower rates of prey delivery due to reduced water flow.

Our ability to sample repeatedly through time while the marshes matured enabled us to begin to track how restoration succession impacts habitat quality from the perspective of a California Halibut. Although water flow and relative temperature differences remained generally consistent through time throughout the wetland complex, the relative abundance of small halibut generally increased with marsh maturation and the associated increases in eelgrass cover. While abundance could be linked to variability in local populations, our data do support the idea that habitat maturity and environmental parameters affect relative halibut abundance in restoration sites. Because large halibut usually did not use the marshes regardless of the presence of eelgrass, we believe that water flow and temperature are more important drivers of habitat selection for this size-class than is eelgrass. Water flow in the channels was faster immediately after restoration due to the larger tidal prism created by increasing the tidal floodplain. Thus, habitat restoration targets were achieved earlier for larger halibut than for smaller ones. In this context, habitat maturity may therefore be more important to smaller halibut (Fox 2013).

Our point-of-capture data showed that California Halibut exhibit a discrete, within-estuary ontogenetic shift in habitat preference, and this habitat preference was supported by our small-scale translocation experiments. It is therefore likely that restored estuaries with heterogeneous landscapes are better suited to supporting a range of halibut size-classes. From our data and local environmental monitoring, we inferred that water flow, the presence/absence of eelgrass, sediment grain size, and temperature gradient are the critical drivers of halibut habitat selection. These environmental factors naturally vary with respect to stream order in tidal creek estuaries like the HBWC, and such variation may be the preferred restoration design for conserving halibut. While full tidal basins may increase the overall availability of subtidal space, such a design results in comparatively less intertidal mudflat area, wider cross-sectional areas with slower water flow, and reduced tidal flushing. It is therefore possible that full tidal basins lack the microhabitat complexity needed to provide the range of high-quality habitat that California Halibut prefer across their life stages (Madon 2002; Nicolas et al. 2010b).

In addition, it is important to note that limited sampling times, low sample sizes, and the semi-quantitative nature of the telemetry data set make it difficult to infer habitat use with these metrics alone. However, by combining these methods with traditional point-in-time sampling, we are better able to understand the spatial trends in the distribution of California Halibut.

As our results and those of prior studies suggest, resource managers should strive to incorporate multiple performance metrics and evaluation criteria into restoration and mitigation monitoring programs (Jones et al. 2014). Point-of-capture methods are limited both temporally and spatially; however, these are typically the sole metrics used to assess fish habitat function in restored estuaries. For example, in our study seven large California Halibut were captured in marshes using beach seines; however, these samples were all taken at tides above approximately 0.61 m and provided no information about whether individuals remained in the marshes. In our study the number of telemetry groups was relatively small, and as our goal was proof of concept, future work should strive to increase the sample sizes. However, even with our limited sample size, the tracking data suggest that large halibut do not remain in marsh habitats for long periods of time nor do they typically move in and out of the marsh habitat on a diel or tidal cycle. Thus, capture-based sampling (particularly when done at low frequency) can heavily bias findings and may miss important temporal trends in habitat use (Fox 2013). As a result, habitat preferences inferred only from catch data should be interpreted with caution. Because active acoustic telemetry can be deployed in all areas in a given wetland complex and across a variety of environmental conditions (e.g. tidal height, water flow, and visibility), telemetry and translocation experiments strongly complement point-of-capture techniques in identifying the habitat types and environmental conditions that are important to California Halibut.

ACKNOWLEDGMENTS

Funding was provided by the Montrose Settlements Restoration Program, California Sea Grant, Los Angeles Rod and Reel Club, and Southern California Tuna Club's Marine Biology Foundation. Logistical support from the California Department of Fish and Wildlife and the Huntington Beach Wetlands Conservancy was critical for this project's success. Numerous people assisted with field work, most notably Kelley Voss, Kady Lyons, Justyn Hinricher, Alayna Petrie, Randall Holder, Nathalia Hernandez, and Jazmyne Gill.

REFERENCES

Allen, L. G., M. M. Yoklavich, G. M. Cailliet, and M. H. Horn. 2006. Bays and estuaries. Pages 119–148 *in* L. G. Allen, D. J. Pondella, and M. H. Horn, editors. Ecology of marine fishes: California and adjacent waters. University of California Press, Berkeley.

Ambrose, R. F., and D. J. Meffert. 1999. Fish-assemblage dynamics in Malibu Lagoon, a small, hydrologically altered estuary in Southern California. Wetlands 19:327–340.

Calabrese, J. M., and W. F. Fagan. 2004. A comparison-shopper's guide to connectivity metrics. Frontiers in Ecology and the Environment 2:529–536.

Calenge, C. M. 2015. Package adehabitat: analysis of habitat selection by animals, version 1.8.18. Available: https://cran.r-project.org/web/packages/adehabitat/index.html. (June 2016).

Conner, L. M., and B. W. Plowman. 2001. Using Euclidean distances to assess nonrandom habitat use. Pages 275–290 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio-tracking and animal populations. Academic Press, San Diego, California.

Dahlgren, C. P., C. A. Layman, G. T. Kellison, A. J. Adams, B. Gillanders, T. S. Miles, I. Nagelkerken, and J. E. Serafy. 2006. Marine nurseries and effective juvenile habitats: concepts and applications. Marine Ecology Progress Series 213:291–295.

Dando, P. R. 2011. Site fidelity, homing, and spawning migrations of flounder *Platichthys flesus* in the Tamar estuary, southwest England. Marine Ecology Progress Series 430:183–196

DeCelles, G. R., and S. X. Cadrin. 2010. Movement patterns of Winter Flounder (*Pseudopleuronectes americanus*) in the southern Gulf of Maine: observations with the use of passive acoustic telemetry. U.S. National Marine Fisheries Service Fishery Bulletin 108:408–419.

Espinoza, M., T. J. Farrugia, and C. G. Lowe. 2011. Habitat use, movements, and site fidelity of the Gray Smoothhound shark (*Mustelus californicus* Gill 1863) in a newly restored Southern California estuary. Journal of Experimental Marine Biology and Ecology 401:63–74.

Fairchild, E. A., N. Rennels, and H. Hunt. 2009. Using telemetry to monitor movements and habitat use of cultured and wild juvenile Winter Flounder in a shallow estuary. Pages 5–22 *in* J. L. Nelson, H. Arrizabalaga, N. Fragoso, A. Hobody, M. Lutcavage, and J. Silbert, editors. Reviews: methods and technologies in fish biology and fisheries—tagging and tracking of marine animals with electronic devices. Springer, Dordrecht, The Netherlands.

Farrugia, T. J., M. Espinoza, C. G. Lowe. 2011. Abundance, habitat use, and movement patterns of the Shovelnose Guitarfish (*Rhinobatos productus*) in a restored Southern California estuary. Marine and Freshwater Research 62:648–657.

Fodrie, E. J. 2006. Quantifying nursery habitat value for the California Halibut, *Paralicthys californicus*: distribution, elemental fingerprinting, and demographic approaches. Doctoral dissertation. University of California, San Diego.

Fodrie, F. J., and L. A. Levin. 2008. Linking juvenile habitat utilization to population dynamics of California Halibut. Limnology and Oceanography 53:799–812.

Fodrie, F. J., and G. Mendoza. 2006. Availability, usage, and expected contribution of potential nursery habitats for the California Halibut. Estuarine, Coastal and Shelf 68:149–164.

Fox, E. J. 2013. Assessing structural and functional recovery in a restored Southern California salt marsh: fish community composition and the diet of juvenile California Halibut. Master's thesis. California State University, Long Beach.

Furey, N. B, M. A. Dance, and J. R. Rooker. 2013. Fine-scale movements and habitat use of juvenile Southern Flounder *Paralicthys lethostigma* in an estuarine landscape. Journal of Fish Biology 82:1469–1483.

Haaker, P. L. 1975. The biology of the California Halibut, *Paralichthys californicus* (Ayres) in Anaheim Bay. U.S. National Marine Fisheries Service Fishery Bulletin 165:186–196.

Hughes, J. E., L. A. Deegan, C. W. Jason, M. J. Weaver, and A. Wright. 2002. The effects of eelgrass habitat loss on estuarine fish communities of southern New England. Estuaries 25:235–249.

Irlandi, E. A., and M. K. Crawford. 1997. Habitat linkages: the effect of intertidal salt marshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. Oecologia 110:222–230.

Jones, K. M. M., P. E. McGrath, and K. W. Able. 2014. White Perch *Morone americana* (Gmelin, 1789) habitat choice and movements: comparisons between *Phragmites*-invaded and *Spartina* reference marsh creeks based on acoustic telemetry. Journal of Experimental Marine Biology and Ecology 455:14–21.

Jordan, F., M. Bartolini, C. Nelson, P. Patterson, and H. Soulen. 1997. Risk of predation affects habitat selection by the Pinfish *Lagodon rhomboides* (Linnaeus). Journal of Experimental Marine Biology and Ecology 208:45–56.

Kimmer, W. J., J. R. Burau, and W. A. Bennett. 1998. Tidally oriented vertical migration and position maintenance of zooplankton in a temperate estuary. Limnology and Oceanography 43:1697–1709.

Kramer, S. H. 1990. Distribution and abundance of juvenile California Halibut, *Paralichthys californicus*, in shallow waters of San Diego County. U.S. National Marine Fisheries Service Fishery Bulletin 89:195–207.

Larson, E. J. 2001. Coastal wetlands-emergent marshes. Pages 483–486 *in* W. S. Leet, C. M. Dewees, R. Klingbeil, and E. J. Larson, editors. California's living marine resources: a status report. California Department of Fish and Game, Sacramento.

Leonard, G. H., J. M. Levine, P. R. Schmidt, and M. D. Bertness. 1998. Flow-driven variation in intertidal community structure in a Maine estuary. Ecology 79:1395–1411.

Love, M. S. 2011. Certainly more than you want to know about the fishes of the Pacific Coast. Really Big Press, Santa Barbara, California.

Love, M. S., and A. Brooks. 1990. Size and age at first maturity of the California Halibut *Paralichthys californicus*, in the Southern California Bight. California Department of Fish and Game Fish Bulletin 174:167–174

Madon, S. 2002. Ecophysiology of juvenile California Halibut, *Paralichthys californicus*, in relation to body size, water temperature, and salinity. Marine Ecology Progress Series 243:235–249.

Madon, S. 2008. Fish community responses to ecosystem stressors in coastal estuarine wetlands: a functional basis for wetlands management and restoration. Wetlands Ecology and Management 16:219–236.

Madsen, J. D., P. A. Chambers, W. F. James, E. W. Koch, and D. F. Westlake. 2001. The interaction between water movement, sediment dynamics, and submersed macrophytes. Hydrobiologia 444:71–84.

Marsh, D. M., K. A. Thakur, K. C. Bulka, and L. B. Clarke. 2004. Dispersal and colonization through open fields by a terrestrial, woodland salamander. Ecology 85:3369–3405.

Merino, G. E., R. H. Piedrahita, and D. E. Conklin. 2007. Effect of water velocity on the growth of California Halibut (*Paralichthys californicus*) juveniles. Aquaculture 271:206–215.

Moser, M. L., M. S. Myers, B. J. Burke, and S. M. O'Niell. 2005. Effects of surgically implanted transmitters on survival and feeding behavior of adult English Sole. Pages 269–274 *in* M. T. Specicato, G. Lembo, and G. Marmulla, editors. Aquatic telemetry: advances and applications. Proceedings of the fifth conference on fish telemetry. Food and Agriculture Organization of the United Nations and COISPA, Ustica, Italy.

Moser, M. L., M. S. Myers, J. E. West, S. M. O'Neill, and B. J. Burke. 2013. English Sole spawning migration and evidence for feeding site fidelity in Puget Sound, U.S.A., with implications for contaminant exposure. Northwest Science 87:317–325.

NOAA (National Oceanic and Atmospheric Administration), U.S. Fish and Wildlife Service, National Park Service, California Department of Fish and Game, California Department of Parks and Recreation, and California State Lands Commission. 2005. Montrose Settlements Restoration Program: programmatic environmental impact statement/environmental impact report. NOAA et al., Long Beach, California.

Nicolas, D., J. Lobry, O. Le Pape, and P. Boët. 2010a. Functional diversity in European estuaries: relating the composition of fish assemblages to the abiotic environment. Estuarine, Coastal, and Shelf Science 88:329–338.

Nicolas, D., J. Lobry, M. Lepage, B. Sautour, O. Le Pape, H. Cabral, A. Uriate, and P. Boët. 2010b. Fish under influence: a macroecological analysis of relations between fish species richness and environmental gradients among European tidal estuaries. Estuarine, Coastal, and Shelf Science 86:137–147.

Nobriga, M., F. Feyrer, R. Baxter, and M. Chotkowski. 2005. Fish community ecology in an altered river delta: spatial patterns in species composition, life history strategies, and biomass. Estuaries and Coasts 28:776–785.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: http://www.R-project.org/. (June 2016).

West, J. M., and J. B. Zedler. 2000. marsh–creek connectivity: fish use of tidal salt marsh in Southern California. Estuaries 23:699–710.

Zedler, J. B. 1996. Coastal mitigation in Southern California: the need for a regional restoration strategy. Ecological Applications 6:84–93.

Zedler, J. B., J. C. Callaway, and G. Sullivan. 2001. Declining biodiversity: why species matter and how their functions might be restored in Californian tidal marshes. BioScience 51:1005–1017.

Zedler, J. B., and R. Langis. 1991. Authenticity: comparisons of constructed and natural salt marshes of San Diego Bay. Ecological Restoration 9:21–25.